

FURTHER STUDIES OF STATIC AND DYNAMIC FUSIMOTOR FIBRES

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(Received 9 March 1964)

The preceding paper (Crowe & Matthews, 1964) has confirmed and extended the finding that there exist two functionally distinct types of fusimotor fibre (Matthews, 1962). They may be distinguished, and have so far been studied, by observing the effect of their stimulation on the response of single primary endings to stretching the muscle at a constant velocity over a distance of several millimetres. The present paper, which is based on the same experiments as the preceding paper, describes the action of the two kinds of fibre on the response of primary endings to some different forms of mechanical stimuli. In addition, certain results are reviewed in relation to the question whether all fusimotor fibres can be reliably classified into static and dynamic fusimotor fibres. Some of the main findings have already been briefly reported (Crowe & Matthews, 1963).

METHODS

The present findings were obtained on the same animals and with the same apparatus as the results of the preceding paper (Crowe & Matthews, 1964) in which the methods employed are fully described. The effects of release, of sinusoidal stretching and of vibration were, however, studied in only about the last half of the series of fifteen cats. For the correlation of the effects of individual fusimotor fibres under static and under dynamic conditions, observations made in an earlier series of similar experiments (Matthews, 1962) have also been included.

RESULTS

Distinctness of subdivision of fusimotor fibres into static and dynamic types

Previous work (Matthews, 1962; Crowe & Matthews, 1964) has shown that some fusimotor fibres produce such distinctive actions on the primary ending that they can be divided into two functionally separate classes, the static and the dynamic fusimotor fibres. Whether, however, all fusimotor fibres can be reliably and usefully so classified is another matter, and remains unknown. In the present experiments the single fusimotor fibres which were studied were initially detected by means of their excita-

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tory action on the primary ending. For this excitatory action to be recognizable it had to be powerful enough to overcome the depressing effect produced on the ending by the simultaneous contraction of extrafusal muscle fibres; ordinary α motor fibres were usually present in all the ventral root filaments which were tested initially for their action on the spindle (Matthews, 1962). Fusimotor fibres with a weak action on primary

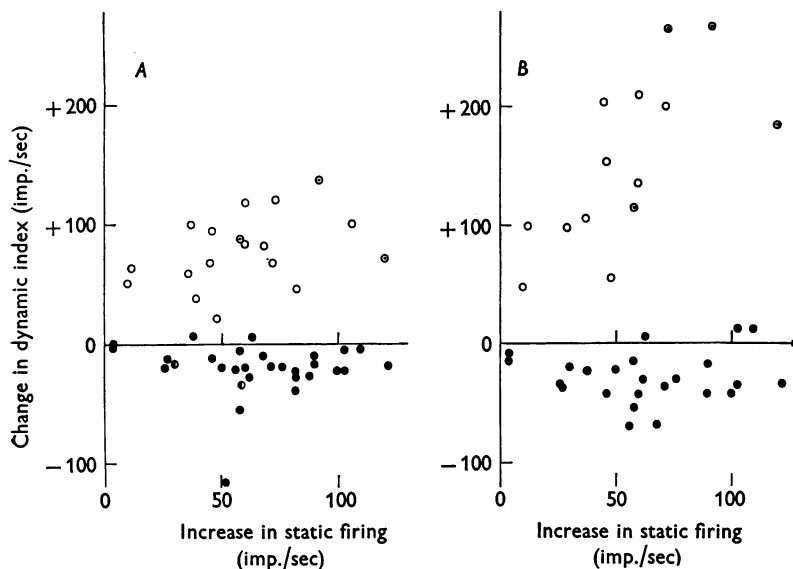


Fig. 1. Scatter diagrams relating the effect of stimulating single fusimotor fibres on the 'dynamic index' of individual primary endings to their effect in exciting the same endings under static conditions. Each point represents one combination of a fusimotor fibre with a primary ending. \bigcirc , \odot , effects classified as due to dynamic fusimotor fibres; \bullet , \odot , effects classified as due to static fusimotor fibres. Ordinate, the change in the dynamic index, from its value without stimulation, produced by the fusimotor stimulation. Abscissa, the increase in the discharge of the ending produced by the fusimotor stimulation when the muscle was at the initial length. *A*, 48 combinations on stretching at 5 mm/sec; *B*, 38 combinations on stretching at 30 mm/sec. The frequency of fusimotor stimulation was usually 100/sec (\bigcirc , \bullet), but occasionally was only 50/sec or 70/sec (indicated by \odot for dynamic fibres, and \odot for static fibres).

endings would not, therefore, have been detected and the present sample of fusimotor fibres will be biased towards those with strong effects, whether under static or dynamic conditions. If different or intermediate types of fusimotor fibre exist, they would not have necessarily been discovered in the present experiments. The matter can only be settled by studying the effects of a number of single γ motor fibres which have been detected and isolated by means of recording their action potential in ventral root filaments on stimulating the muscle nerve. Meanwhile, however, it

seems useful to discuss how distinctly those fusimotor fibres which were isolated can be classified into two groups.

The criterion used to classify the different fusimotor fibres was their effect on the 'dynamic index' of the primary ending on stretching the muscle at 5 mm/sec. The dynamic index is an arbitrary measure of the response of the ending to the dynamic component of the stimulus. It is defined as the slowing of the discharge of the ending occurring on completion of the dynamic phase of stretching, and largely for practical reasons was measured over the first 0.5 sec. (Jansen & Matthews, 1962; Matthews, 1962; Crowe & Matthews, 1964). Fusimotor fibres which significantly increased the dynamic index were classified as dynamic fusimotor fibres and those which decreased or did not alter it were classified as static fusimotor fibres. Most of the fusimotor fibres could be confidently classified by this criterion alone. The classification could be improved by also taking into account the effect of stimulation of the fusimotor fibre on the discharge of the ending when the muscle was at a constant length. This increase in the discharge was measured at the initial length of the muscle or when it had been extended by 1–2 mm to remove any slack. Figure 1*A* shows, for every combination studied of a fusimotor fibre with a primary ending, the change in the dynamic index produced by fusimotor stimulation plotted against the increase in the static discharge. Most points fall clearly into one or other of two groups. In one group (\circ , \odot) the dynamic index was increased above its value without stimulation, and this increase was larger the greater the stimulating effect of the fusimotor fibre under static conditions; these points may be considered to be due to stimulation of dynamic fusimotor fibres. In the other group of points (\bullet , \bullet) the dynamic index was usually slightly below its value without stimulation, though there was no progressive relation between this slight decrease and the magnitude of the action of the fusimotor fibre under static conditions; these points may be considered to be due to stimulation of static fusimotor fibres, as also may the points just above the *X*-axis and accompanied by an appreciable increase in the static discharge. Similar results were obtained on stretching at higher velocities, as illustrated in Fig. 1*B* which is similar to Fig. 1*A* except that the velocity of stretching was 30 mm/sec. Figure 1 shows that the classification of fusimotor fibres could actually be made more confidently on stretching at 30 mm/sec than at 5 mm/sec, but this velocity was not used in every experiment. Figure 1 shows also that the dynamic fusimotor fibres usually produce a greater increase in the dynamic index on stretching at 30 mm/sec than at 5 mm/sec, that is to say that their stimulation increased the slope of the relation between the dynamic index and the velocity of stretching (Crowe & Matthews, 1964). On altering the frequency of stimulation of the fusimotor fibres, qualitatively similar

effects were usually produced, and the fusimotor fibres could be as certainly classified (cf. Fig. 4, Crowe & Matthews, 1964). In one experiment, however, at frequencies of stimulation of 70/sec or below, the action of the fusimotor fibre was weak and appeared to be that of a static fusimotor fibre, while at higher frequencies of stimulation its action was that of a typical dynamic fusimotor fibre. This fibre was classified as a dynamic fusimotor fibre; in the plots of Fig. 1 it gave rise to the lowest of the open circles. It may be concluded, however, that fusimotor fibres in the present sample could be classified reasonably confidently into static and dynamic fusimotor fibres, in spite of the fact that the absolute magnitude of their action varied considerably. Whether this would apply to all fusimotor fibres is unknown, and it may be noted that the validity of the classification is most apparent for those fusimotor fibres which produced powerful effects on the spindle.

*Constancy of action of single fusimotor fibres on
different primary endings*

Hunt & Kuffler (1951) showed that a single fusimotor fibre may influence more than one primary ending and since a muscle spindle usually contains only a single primary ending (Boyd, 1962) it follows that a single fusimotor fibre may supply more than one muscle spindle. It seemed important to enquire whether the action of individual fusimotor fibres in different spindles was of the same kind, that is, either static or dynamic, or different. In the present experiments, after isolation of single fusimotor fibres by means of their action on one primary ending, their action was tested on various other primary endings. In about 180 such trials eleven endings were found to be influenced in addition to the original ones. The effect of any individual fusimotor fibre, however, proved to be constant as illustrated in Figs. 2 and 3. In Fig. 2 a single fusimotor fibre produced a typical dynamic effect on three different primary endings (compare with Fig. 1, Crowe & Matthews, 1964). In Fig. 3, from a different experiment, another single fusimotor fibre produced a typical static effect on three different primary endings; it will be noticed, however, that the strength of the effects produced on the various endings differed. Besides those illustrated, two fusimotor fibres were found each of which had a dynamic action on two different primary endings; another fusimotor fibre had a static action on four different primary endings, and another similarly influenced three different endings. The probability of such a constancy of the effects of individual fusimotor fibres being found by chance is under 0.1 %.

The probability that the observed results occurred by chance was first calculated on the basis of the assumption that the action of a fusimotor fibre on a second primary ending was as likely to be static as dynamic. This gave a probability of 0.05 %. The calculation was then

repeated assuming that the probability of a fibre having a static effect was twice that of its having a dynamic effect; for this was the relative frequency at which the two kinds of fibres were isolated. This gave a probability of 0.07 %. It is not known whether the relative frequency of isolation of the two kinds of fibre reflected the true frequency of their occurrence, or depended upon the method of selection (*vide supra*). It is unlikely to have depended upon a differential death rate of the two kinds of fibre in the course of subdividing the root

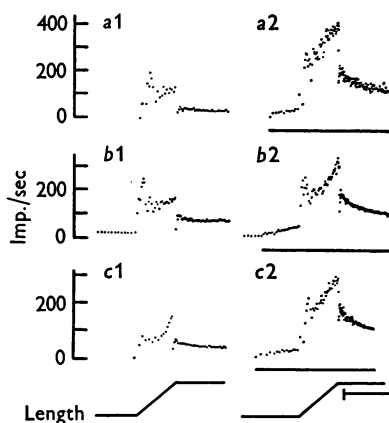


Fig. 2. The effect on three different primary endings of stimulating the same single fusimotor fibre. This fibre had a dynamic action on all three endings. *a1*, *b1*, *c1*, responses of endings on stretching the muscle 6 mm at 30 mm/sec in the absence of stimulation. *a2*, *b2*, *c2*, responses on similar stretching applied during stimulation of fusimotor fibre at 50/sec (see bars beneath records). Each action potential is represented by a dot, the vertical displacement of which is proportional to the reciprocal of the time interval since the immediately preceding action potential (i.e. the instantaneous frequency; see scales, which are not all identical). The 1 sec calibration does not apply to the periods of dynamic stretching which are on more open time scales. (Records retouched.)

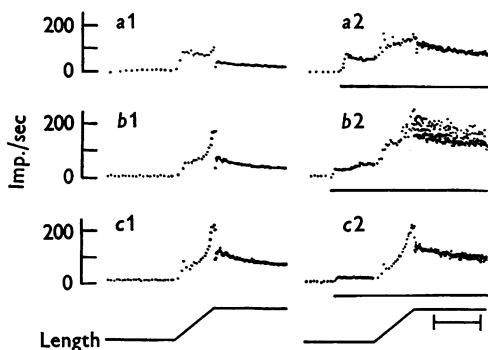


Fig. 3. The effect on three different primary endings (*a*, *b*, *c*) of stimulating the same single fusimotor fibre. This fibre had a static action on all three endings. Different experiment from that of Fig. 2, but the records are similarly arranged and labelled. The muscle was stretched 6 mm at 30/sec. The frequency of fusimotor stimulation was 135/sec. Calibration, 1 sec. (Records retouched.)

filaments, for static effects were commoner than dynamic effects on stimulating the moderately thick ventral root filaments which were tested initially.

It must be mentioned, however, that one of the fusimotor fibres which was found to influence more than one ending was the slightly anomalous dynamic fusimotor fibre already mentioned, which only produced a clear-cut dynamic effect on one ending when the frequency of stimulation was 100/sec or above; on the other ending that it influenced it produced a typical dynamic effect whatever the frequency of stimulation. If this fusimotor fibre is omitted from the calculation, then the probability of the observed results being obtained by chance becomes either 0.1 or 0.2 %, depending upon the assumptions made about the frequency of occurrence of the two kinds of fusimotor fibre.

It may be noted that on three occasions a static fusimotor fibre was found to excite powerfully a secondary ending (identified by the conduction velocity of its afferent; Matthews, 1963). The behaviour of these secondary endings during fusimotor stimulation was similar to that of primary endings excited by a static fusimotor fibre, and they were rather insensitive to the dynamic stimulus of being stretched, just as they were in the absence of stimulation (cf. Matthews, 1963). Thus secondary endings can be excited by static fusimotor fibres, but whether or not they are also significantly excited by dynamic fusimotor fibres is unknown.

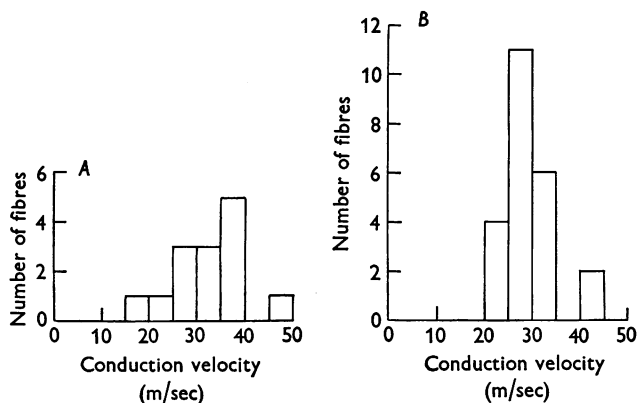


Fig. 4. Histograms of the distributions of the conduction velocities of all the fusimotor fibres which were isolated. (Results from Matthews, 1962 included.) A, fourteen dynamic fusimotor fibres; B, twenty-three static fusimotor fibres.

Distribution of conduction velocities of different fusimotor fibres

The conduction velocity of each fusimotor fibre studied was determined by stimulating the muscle nerve and recording the resulting action potential of the fibre from the ventral root filament (for fuller details see Matthews, 1963). In extension of the earlier findings no clear-cut difference has been observed between the conduction velocities of the static and of the dynamic fusimotor fibres. This is illustrated by the histograms in Fig. 4. On average, the conduction velocity of dynamic fusimotor fibres ($32.9 \text{ m/sec} \pm 1.8 \text{ S.E. of mean}$) was slightly greater than that of static fusimotor fibres ($29.3 \text{ m/sec} \pm 1.2, \text{ S.E. of mean}$); but the overlap in conduction

velocity of the two kinds of fibre was too great for it to be possible to identify a fibre by this means. The diameters of the two kinds of fibre presumably also overlap considerably, for the conduction velocity of medullated fibres varies with their diameter (Hursh, 1939).

It cannot be decided whether or not any of the fusimotor fibres studied in the present experiments also supplied extrafusal muscle fibres, as may some fibres to the first deep lumbrical muscle of the cat (Bessou, Emonet-Denand & Laporte, 1963*a*). B. Appelberg and F. Emonet-Denand (personal communication) have recently found that stimulation of some small α motor fibres to the soleus of the cat may cause so weak a contraction that it is not readily detected myographically (tension produced probably well under 1 g wt.). Contraction of the muscle could, however, be observed when the surface of the muscle was exposed, and a diphasic electrical potential could be recorded with surface electrodes. Such contraction would probably not have been detected in the present experiments, which were based on the assumption that repetitive activation of single motor units would produce tensions of about 10 g wt., recorded isometrically (Matthews, 1962) and tensions below 1 g wt. on stimulation of single fusimotor fibres were not sought. In one experiment repetitive stimulation of a filament containing a dynamic fusimotor fibre did produce a tension of 1.2 g wt.; at the time this was attributed to the contraction of some hip muscles which had not been fully denervated, but whether this was the correct explanation cannot now be determined. The electromyogram was not recorded in the present experiment, nor was the surface of the muscle exposed. The present analysis of the effects of different fusimotor fibres on the behaviour of the primary ending is relatively little affected by whether or not some of the fusimotor fibres also supplied extrafusal fibres.

*Response of primary endings on release of extension
during fusimotor stimulation*

In the absence of fusimotor activity primary endings stop firing abruptly at the beginning of a slow release of the muscle from a previously applied extension (Harvey & Matthews, 1961) and do not begin firing again until well after the release is complete (Matthews, 1933). During stimulation of fusimotor fibres the primary endings usually continued to discharge throughout the period of releasing the muscle a distance of 6 mm at 5 mm/sec. But characteristic differences were then observed between the response of the primary ending on stimulating static fusimotor fibres and on stimulating dynamic fusimotor fibres, even though the two kinds of fibre often produced the same increase in the discharge of the primary ending when the muscle was at a constant length. This is illustrated in Fig. 5 which shows the response of two different primary endings, chosen for illustration because the effects on them of the fusimotor stimulation at a constant muscle length were about the same. During stimulation of the dynamic fusimotor fibre there was an abrupt initial drop in the frequency of discharge of the ending at the beginning of the release, and the discharge then tended to stay relatively constant until the releasing was completed. During the stimulation of the static fusimotor fibre, however, there was no initial drop in the discharge but the frequency fell pro-

gressively as the release progressed. Such a difference in the effects of the two kinds of fusimotor fibre has been found consistently on studying eleven combinations of a static fusimotor fibre with a primary ending and nine combinations of a dynamic fusimotor fibre with a primary ending, and releasing the muscle 6 mm at 5 mm/sec. The higher the frequency of stimulation of the fusimotor fibre the greater was the discharge of the ending during the release, but the different actions of the two kinds of fusimotor fibres were still clear. On lower frequencies of stimulation (70/sec or below) the ending was often completely silent during the release on stimulating dynamic fusimotor fibres, and this sometimes occurred also on high frequency stimulation. During stimulation of static fusimotor fibres complete cessation of the discharge during the releasing hardly ever occurred

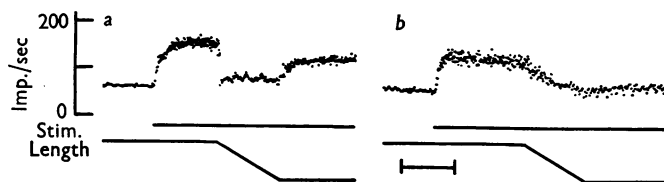


Fig. 5. Typical responses on releasing a stretched muscle during fusimotor stimulation. *a*, response of one primary ending during stimulation of a dynamic fusimotor fibre at 70/sec for period shown by bar. *b*, response of another ending during stimulation of a static fusimotor fibre at 70/sec. In the absence of stimulation both endings stopped firing abruptly at the beginning of the release. The muscle was released 6 mm at 5 mm/sec. The 1 sec calibration applies to the whole of both records. (Records retouched.)

even when the frequency of stimulation was low. The different effects of the two kinds of fusimotor fibre were not investigated quantitatively, nor were a range of velocities of release employed. A few tests of the effect of releasing an extension of 1 mm at 1 mm/sec suggested that the differences were then less marked, though still discernible. On releasing at 5 mm/sec, the different effects were sufficiently obvious for the fusimotor fibres to be confidently identified by this means. The different effects may be interpreted either in terms of the contractile properties of the intrafusal fibres supplied by the two kinds of fusimotor fibre (those supplied by the static fusimotor fibres being 'faster' than those supplied by the dynamic fusimotor fibres) or in terms of the visco-elastic properties of the regions of the two kinds of intrafusal fibre on which the branches of the primary ending lie (i.e. that one region is a largely undamped elastic element, and that the other region has visco-elastic properties like the rest of the fibre).

Response to sinusoidal stretching

The results described so far were obtained using stretches of 6 mm applied at a constant velocity. In addition the effects of smaller stretches applied sinusoidally were studied (cf. Lippold, Redfearn & Vučo, 1958); among other things these stretches provide a rather direct contrast of the effect on the spindle of stretching and of releasing the muscle. The sinusoidal stretches were produced by feeding the electro-magnetic stretcher from a low-frequency oscillator (Servo-Mex, TWG 100). The frequency of the stretching was varied from 1 to 10 c/s and its amplitude (half the total extent) was either 0.5 or 0.05 mm. The initial length of the muscle was

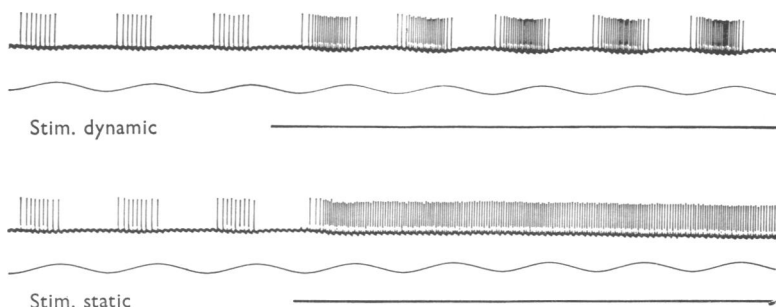


Fig. 6. Effect of fusimotor stimulation on the response of a primary ending to sinusoidal stretching. The records are conventional, and show spikes on a linear time scale. The stretching was at 3 c/s and its amplitude (half its total extent) was 0.5 mm. The stimulation, indicated by bars, was at 100/sec in both cases. The sinusoidal records show the imposed length.

adjusted so that the muscle remained taut at all phases of the cycle, at any rate when the frequency was below 5 c/s. As the results were only analysed qualitatively the wave form of the actual movement was not checked for harmonic distortion, but this seems unlikely to have been significant.

During sinusoidal stretching characteristic differences were again observed in the behaviour of the primary ending on stimulating the two kinds of fusimotor fibre. These differences are illustrated in Fig. 6 which is a conventional record, consisting of spikes against time, of the discharge of the ending during 0.5 mm amplitude stretching the muscle at 3 c/s. In the absence of fusimotor stimulation the ending fired eight or nine impulses each time the muscle was stretched, but was silent as the muscle was released. During stimulation of a dynamic fusimotor fibre the discharge during the stretching increased to about twenty-five impulses, which were at a much higher frequency than before, but the ending was still silent during the release. However, each burst started earlier and ended later than without stimulation. During stimulation of a static

fusimotor fibre, which influenced the same ending, the mean frequency of discharge of the ending increased considerably, but the ending now fired throughout the whole cycle of stretch and release, and there was relatively little change in its discharge in response to the rhythmic mechanical stimulus. Figure 7 shows, by means of the frequency display, the effects of fusimotor stimulation on the response of another ending to a stretch of 0.05 mm amplitude. During stimulation of the dynamic fusimotor fibre the ending fired throughout the whole cycle, but its frequency of dis-

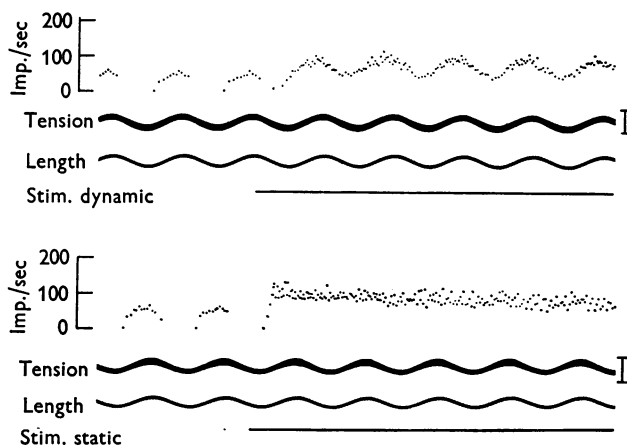


Fig. 7. Effect of fusimotor stimulation on the response of a primary ending to small amplitude (0.05 mm) sinusoidal stretching at 2 c/s. The records show the instantaneous frequency of discharge of the ending on a linear time scale. Different experiment from that of Fig. 6. The frequency of stimulation was 100/sec for the dynamic fibre and 50/sec for the static fibre. Tension marker 20 g. wt. (Records retouched.)

charge varied markedly with the phase of the stretching. During stimulation of the static fusimotor fibre the ending was unaffected by the stretching.

Such results were typical of those obtained on studying four combinations of a static fibre and a primary ending and four combinations of a dynamic fibre and a primary ending, and are independent of the mean length of the muscle. It will be appreciated, however, that Figs. 6 and 7 have been selected so as to illustrate the contrast between the effects of the two kinds of fusimotor fibre, and the qualitative difference was not invariably so marked. As would be expected, on increasing the frequency or the amplitude of the oscillation the change in the discharge of the ending in relation to the stretch became more pronounced, and could be appreciable even during stimulation of a static fusimotor fibre, particularly if the stimulation was of low frequency; sometimes then the

ending would be silent during the release. Also, as the frequency of stimulation of a dynamic fusimotor fibre was increased or the frequency or amplitude of oscillation was decreased, so silence during release (as in Fig. 6) could be replaced by low-frequency firing (as in Fig. 7). But even in the absence of a comprehensive quantitative analysis there was no doubt that in general sinusoidal stretching caused much more marked changes in the discharge of the ending during stimulation of dynamic fusimotor

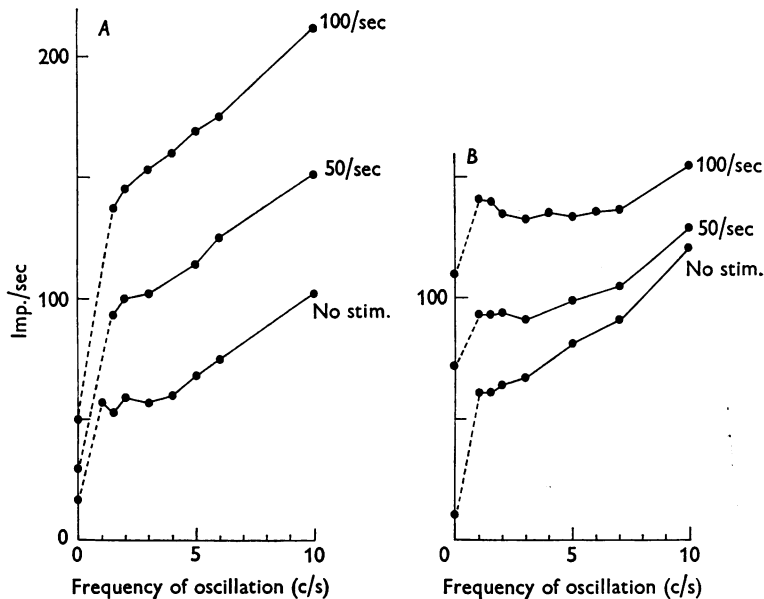


Fig. 8. Relation between the peak frequency of discharge of a primary ending during sinusoidal stretching and the frequency of stretching. *A*, during stimulation of a dynamic fusimotor fibre. *B*, same primary ending during stimulation of a static fusimotor fibre. The points at zero frequency of oscillation show the discharge in the absence of stretching. The amplitude of stretching was 0.5 mm. Same experiment as Fig. 6.

fibres than it did during stimulation of static fusimotor fibres. The different action of the two kinds of fusimotor fibre were further displayed by plotting the peak frequency of discharge of the ending during the stretching against the frequency of oscillation. As illustrated in Fig. 8 the peak discharge increased more rapidly with the frequency of oscillation during stimulation of dynamic fusimotor fibres than it did during stimulation of static fibres.

Phase of response. As can be seen in Figs. 6 and 7 the peak frequency of firing of the ending occurred before the peak tension or length of the muscle was reached, and this was regularly found both in the presence and absence of fusimotor stimulation. Thus the response of the primary ending may be said to be 'phase advanced' on the sinusoidal stretching

(Lippold *et al.* 1958), as occurs for all systems that respond to velocity as well as to displacement. Our records were not taken in such a manner as to permit accurate determinations of phase angles, particularly for the higher frequencies of oscillation (the film moved too slowly, and the peak of the spindle response was not always accurately identifiable). Some measurements were, however, made of the phase angle of the response to low-frequency oscillation. These showed that the phase angle did not change greatly as the frequency of stimulation of a dynamic fusimotor fibre was increased, even though this increases the response of the ending to the stimulus of velocity (Crowe & Matthews, 1964), and so in the first place might be expected to increase the phase advance. The explanation of this apparent discrepancy is probably that, as measured during stretching, stimulation of dynamic fusimotor fibres tends to increase the sensitivity of the primary ending to the displacement component of a stimulus, as well as to the velocity component (Crowe & Matthews, 1964); it is the ratio of these two components of response which determine the phase angle. During stimulation of static fusimotor fibres, in those cases in which there was a detectable modulation of the discharge, the response was also appreciably phase advanced on the stretching. Endings made largely insensitive by static fusimotor stimulation to the velocity component of the stimulus would be expected to show rather little modulation of their discharge on small amplitude stretching (cf. Fig. 7), and so responses with little or no phase advance would not usually be expected to be measurable under the present conditions. (Under static conditions, increasing the length of the muscle by 1 mm only rarely increased the discharge of the ending by more than 10 impulses/sec, either in the presence or absence of fusimotor stimulation.) It cannot yet be accepted that a primary function of fusimotor fibres is to change the phase angle of the response of the primary ending as was tentatively suggested (Jansen & Matthews, 1962), though they can clearly control the amplitude of the response of the ending to sinusoidal stretching. Further study of such matters is encouraged by the finding (illustrated in Fig. 7) that for small amplitudes of stretching applied during fusimotor stimulation the ending fires continuously without a silent period and that the envelope of the frequency response is approximately sinusoidal.

Effect of fusimotor stimulation on response of ending to vibration

On increasing the frequency of sinusoidal stretching of a muscle its muscle spindle afferents fire fewer and fewer impulses for each cycle of the oscillation until there is only one per cycle. On further increasing the frequency of the oscillation, or vibration as it may now be called because of its high frequency, the ending continues to fire one impulse per cycle until a critical frequency is reached, beyond which it fails to follow the vibration (Granit & Henatsch, 1956; Bianconi & van der Meulen, 1963). Granit & Henatsch (1956) have shown that this critical following frequency varies from spindle to spindle, and may be increased by increasing the initial tension on the muscle or the amplitude of the vibration. More significantly, they found that the critical following frequency could be greatly increased by fusimotor activity; in their experiments the fusimotor activity was that occurring naturally in cats with intact ventral roots. We initially anticipated that this effect would be produced by stimulation of dynamic fusimotor fibres only, but it has turned out that both kinds of fusimotor fibre can increase the frequency at which primary endings can follow vibration, and we have not been able to distinguish

between their activity in this respect. This action of fusimotor stimulation is illustrated in Fig. 9. For the whole of both records a vibration at 350 c/s of about $10\ \mu$ total displacement was applied to the tendon of soleus. In the absence of fusimotor stimulation the endings were being weakly excited by the vibration and fired irregularly with the various impulses occurring at certain 'preferred frequencies', which were subharmonics of the vibration frequency. On stimulation of the fusimotor fibres the discharge of the endings increased to 350/sec and became quite regular, showing that they were then being excited by the vibration to discharge one impulse per cycle. In the absence of fusimotor stimulation the ending of Fig. 9*a*



Fig. 9. Examples of the sensitization of primary endings to vibration by fusimotor stimulation. Throughout the whole of both records the tendon of soleus was vibrated at 350 c/s with a total displacement of about $10\ \mu$. *a*, stimulation of a dynamic fusimotor fibre at 70/sec for period shown by bar. *b*, from another experiment, stimulation of a static fusimotor fibre at 70/sec. Frequency display as in Fig. 2. Time calibration, 1 sec.

would not follow a vibration of slightly greater amplitude above 270/sec and that of Fig. 9*b* would not follow above 220/sec. Fusimotor stimulation in the absence of vibration increased the discharge of the ending of Fig. 9*a* by 44/sec and that of Fig. 9*b* by 70/sec. Thus the increase in the frequency at which vibration could be followed was greater than the increase in the discharge of the endings produced by fusimotor stimulation in the absence of vibration. An increased sensitivity to vibration was found in every case on testing seven combinations of a dynamic fusimotor fibre and a primary ending, and four combinations of static fibre and primary ending, but the precise increase in the critical following frequency was not always determined. Increasing the frequency of stimulation of either kind of fusimotor fibre usually increased the maximum frequency of vibration of a particular amplitude which could be followed. In view of the variability of the responses of different spindles there appeared to be no immediate benefit in studying in more detail the interaction of the various factors which influenced the frequency of vibration which the ending could follow (i.e. initial tension, amplitude of vibration, frequency of fusimotor stimulation).

*Effect of simultaneous stimulation of a static
and of a dynamic fusimotor fibre*

Presumably in the intact animal, static and dynamic fusimotor fibres frequently discharge at the same time and modify each other's action. It seemed of interest to compare the effects of stimulating, separately and in combination, a fusimotor fibre of each kind, both of which influenced the same primary ending. This was achieved in four experiments and was done both with the muscle at a constant length and while it was stretched by 6 mm at velocities from 5 to 50 mm/sec. The results proved, however, to be unremarkable. When the muscle was at a constant length, simultaneous stimulation of both fusimotor fibres together produced a greater

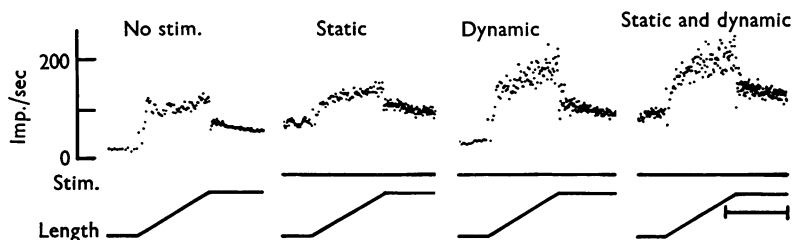


Fig. 10. Examples of the effects of stimulating, separately and together, a static fusimotor fibre and a dynamic fusimotor fibre, both at 70/sec. Frequency display and time scale as in Fig. 2. The muscle was stretched 6 mm at 10 mm/sec. Time calibration, 1 sec.

increase in the discharge of the ending than did stimulation of either alone (i.e. summation). The increase in the discharge produced by the combined stimulation was, however, less than the sum of the increases produced by stimulating the two fusimotor fibres separately (i.e. partial summation only, which is occlusion). Similar results were obtained on stretching during stimulation (Fig. 10), when the frequency of discharge during the dynamic phase of stretching was slightly greater with the combined stimulation than with stimulation of either fusimotor fibre alone. Again, on combined stimulation the increase in the discharge above the level without stimulation was slightly less than the sum of the increases produced by individual stimulation. (These comparisons were most reliably made by comparing the mean frequencies of discharge during the dynamic phase of stretching.) Some occlusion was found under both static and dynamic conditions in all four experiments, but it varied in amount. The effect of simultaneous stimulation of two fusimotor fibres of the same kind was not tested, but the occurrence of some occlusion in this case also would not be remarkable. The point which does seem worth stressing is that the absolute frequency of discharge of the ending occurring during the

dynamic phase of stretching while stimulating a dynamic fusimotor fibre was not reduced by stimulating a static fusimotor fibre in addition. This makes it unlikely that there is a significant degree of mechanical unloading of one kind of intrafusal fibre on contraction of the other kind of fibre, at any rate under the conditions of the present experiments (large amplitude stretching, high-frequency stimulation of single fusimotor fibres); the occurrence of such unloading under other conditions cannot, however, be excluded.

Time course of effects of fusimotor stimulation

We have the impression, unsubstantiated by precise measurement, that in general the effects of stimulation of static fusimotor fibres started and stopped more abruptly than those of stimulation of dynamic fusimotor fibres, thus suggesting that the speeds of contraction of the intrafusal muscle fibres supplied by the two kinds of fusimotor fibre are different. The impression is based on the inspection of a very large number of records obtained with the frequency display; precise observation was hindered by the considerable variation between different experiments, and in a single experiment on varying the frequency and total duration of fusimotor stimulation and the initial length of the muscle. It appeared, however, that in general static fusimotor fibres, in comparison with dynamic fusimotor fibres, caused the discharge of the ending to rise more abruptly at the beginning of repetitive stimulation and fall more abruptly with cessation. Our records did not, however, permit any direct correlation to be made between the response of the ending and the precise period of stimulation, since the individual stimuli were not recorded and the film speed was too slow (1 cm/sec); the latency of the effects could not, therefore, be determined. Sometimes on beginning to stimulate a static fusimotor fibre with the muscle at a constant length the discharge of the primary ending temporarily slightly overshoot its later approximate equilibrium value (cf. Fig. 1, Matthews, 1962); this effect was not seen on stimulating dynamic fusimotor fibres. It was also noted that the onset and offset of the sensitization to vibration produced by fusimotor stimulation was more abrupt for static than for dynamic fibres; on cessation of stimulation of static fusimotor fibres the ending often responded less well to the vibration than it had done before stimulation, while this was not seen for the dynamic fusimotor fibres (cf. Fig. 9).

We have confirmed the earlier observation (Matthews, 1962) that the discharge of a primary ending tends to be appreciably less regular during stimulation of a static fusimotor fibre than during stimulation of a dynamic fusimotor fibre. On occasion it could be seen that during stimulation of a static fusimotor fibre there was a burst of two or three sensory impulses for each stimulus to the fusimotor fibre, suggesting that the irregularity depended upon disturbance of the otherwise regular rhythm of discharge of the ending by an unfused tetanic contraction of the intrafusal fibres. In addition, 'driving', in which the ending discharges one spike for each stimulus to the fusimotor fibre (Kuffler, Hunt & Quilliam, 1951), has been seen for six out of thirty combinations of a static fusimotor fibre with a primary ending but never in eighteen combinations of a dynamic fusimotor fibre with a primary ending.

DISCUSSION

Nearly all the fusimotor fibres which were studied could be confidently classified as either static or dynamic fusimotor fibres by observing their action on the response of the primary ending to stretching the muscle at various velocities. The significance of this classification was increased by

finding that when a fusimotor fibre was found to influence more than one ending then it had the same action, whether static or dynamic, on all the endings influenced. But, because the fusimotor fibres were initially detected by observing their action on a primary ending, different or intermediate types of fusimotor fibre might not have been discovered if their excitatory action on the primary ending were only weak. None the less, it seems probable that the present functional classification of fusimotor fibres corresponds to the histological classification made by Boyd (1962) of fusimotor fibres into γ_1 and γ_2 fibres, supplying respectively the nuclear-bag and the nuclear-chain intrafusal muscle fibres. Without direct evidence several authors (Appelberg, 1962; Bianconi & van der Meulen, 1963; Cooper, 1961; Granit & van der Meulen, 1962; Laporte, 1962; Jansen & Matthews, 1962) have attributed the remarkable sensitivity of the primary ending to dynamic stimuli to its branches on that remarkable structure, the nuclear-bag region of the nuclear-bag fibres, rather than to its branches on the central regions of the nuclear-chain fibres. If this supposition is correct then the dynamic fusimotor fibres, which increase the dynamic sensitivity of the primary ending, can be expected to correspond to the γ_1 fibres which supply the nuclear-bag intrafusal fibres; the static fusimotor fibres would then correspond to the γ_2 fibres. But the identification of dynamic fusimotor fibres with γ_1 rather than with γ_2 fibres is certainly not yet firmly established. Nor is such identification favoured by the provisional finding that the contraction of the intrafusal fibres supplied by the static fibres is 'faster' than that of those supplied by the dynamic fibres, for on histological grounds Boyd (1962) suggested that the chain fibres should be slower than the bag fibres. It would have greatly simplified the correlation of the anatomical and physiological classifications if the conduction velocities of the static and of the dynamic fusimotor fibres had been found to be different, for measured at the muscle spindle itself the diameter of γ_1 fibres is greater than that of γ_2 fibres (Boyd, 1962). It has not been established, however, whether the stem fibres giving rise to the γ_1 and γ_2 fibres also differ in size. The suggestion that they regularly do so (Boyd & Davey, 1962; Boyd & Eccles, 1963) has not been confirmed for a lumbrical muscle by M. N. Adal and D. Barker (personal communication) who have succeeded in tracing individual motor fibres from the spindle back into the main nerve trunk.

Barker (1962; Barker & Cope, 1962) has suggested that the histological classification of fusimotor fibres into two groups only is an over-simplification, and he considers that individual fusimotor fibres commonly supply both nuclear-bag and nuclear-chain intrafusal muscle fibres. The present experiments, while emphasizing that there are great functional differences between different fusimotor fibres, do not show decisively

whether or not individual fusimotor fibres supply only one kind of intrafusal muscle fibre. It seems probable that any fusimotor fibre which has branches on a nuclear-bag intrafusal muscle fibre would behave as a dynamic fusimotor fibre even if it also had a few branches on a nuclear-chain fibre (cf. the slightly anomalous fibre described earlier). But the fact that for the whole population of dynamic fusimotor fibres (Fig. 1) their excitatory action under static and under dynamic conditions increased together suggests that their action arose from contraction of a single kind of intrafusal fibre only, rather than from both kinds of intrafusal fibre contracting in varying relative proportions. However, preliminary results obtained with a cat lumbrical muscle (P. Bessou, F. Emonet-Denand and Y. Laporte, personal communication) suggest that the division of fusimotor fibres into static and dynamic types may not always be as clear-cut as it has appeared to be in the present experiments on a single muscle, with a possibly biased method of selection of the fusimotor fibres. Moreover, Bessou, Emonet-Denand & Laporte (1963*b*) have shown that in this muscle a dynamic effect, similar to that described in the present work, may be produced on some primary endings by stimulating slow α motor fibres which also supply extrafusal muscle fibres.

It was satisfactory to find that the action of static and dynamic fusimotor fibres on the primary ending differed on releasing the muscle, and on stretching it sinusoidally by a small amount, as well as on stretching it linearly by a large amount. Both kinds of fusimotor fibres, however, sensitized the primary ending to vibration, and this may be important for understanding the intimate mechanism of the spindle. Bianconi & van der Meulen (1962) suggested that the ability of a spindle afferent ending to follow vibration means that its receptor terminals lie on a relatively undamped or non-viscous region of intrafusal fibre, for otherwise, the vibratory deformation might not be transmitted to the receptor. Thus one interpretation of the present findings would be that the central regions of both the nuclear-bag and the nuclear-chain fibres are relatively undamped, at any rate compared to their polar regions, and this suggestion is quite compatible with the structure of the fibres (discussed in Matthews, 1964). If this should be so, the differences in the action on the primary ending of the two kinds of fusimotor fibre seem more likely to be due to differences in the contractile properties of the two kinds of intrafusal fibre, rather than due to differences in the visco-elastic properties of their central regions. Indeed, most of the present findings would be explained if, in comparison with the contraction of the nuclear-chain fibres, the contraction of the nuclear-bag fibres was relatively slow and developed a tension appreciably affected by the speed at which the muscle fibre was shortening or being extended (cf. Crowe & Matthews, 1964). But the

vibration experiments do not prove that the central region of the nuclear-chain fibre is relatively undamped since explanation of the present findings can also be developed without this assumption.

SUMMARY

1. Further observations have been made of the effects of stimulating fusimotor fibres on the behaviour of primary endings of muscle spindles in the soleus muscle of the anaesthetized cat.

2. A comparison was made of the effect of stimulating each of the fusimotor fibres isolated on the response of single primary endings to stretching the muscle by 6 mm at various velocities. In spite of variation in their excitatory effect nearly every fusimotor fibre fell cleanly into one or other of two groups, corresponding to the static and dynamic fusimotor fibres previously described (Matthews, 1962). However, owing to the method of detection and isolation of the fusimotor fibres the existence of different or intermediate types of fusimotor fibre has not been excluded.

3. Occasionally it proved possible to study the action of a fusimotor fibre on more than one primary ending. Any particular fusimotor fibre was then found to have the same action, whether static or dynamic, on all the primary endings that it was found to influence.

4. Studied in the nerve trunk, there was almost complete overlap in the conduction velocities, and therefore presumably also of the diameters, of the two kinds of fusimotor fibre.

5. Single fusimotor fibres were stimulated during release of the muscle from a previously applied extension of 6 mm. At the beginning of the release there was an abrupt fall in the frequency of discharge of a primary ending during stimulation of dynamic fusimotor fibres, but not during stimulation of static fusimotor fibres.

6. Low-frequency (1–10 c/s) small amplitude (0.5 or 0.05 mm) sinusoidal stretching of the muscle caused much greater changes in the discharge of the ending during stimulation of dynamic fibres than during that of static fibres.

7. Stimulation of either kind of fusimotor fibres, however, sensitized the primary ending to vibration (frequency over 200/sec, amplitude below 10μ), permitting it to discharge at the same frequency as the vibration up to higher frequencies than before.

8. Simultaneous stimulation of a static fibre and of a dynamic fibre, both of which influenced the same primary ending, produced a slightly greater excitatory effect than did either alone.

9. The results are discussed in relation to the structure of the spindle. It seems probable that the functional classification of fusimotor fibres into

static and dynamic fusimotor fibres corresponds to the histological classification of fusimotor fibres into γ_1 and γ_2 fibres. Indirect arguments suggest that the dynamic fibres correspond to γ_1 fibres and static fibres to γ_2 fibres, but this is certainly not yet firmly established.

We wish to thank Mr E. T. Giles and Mr P. Searce for technical assistance. P.B.C.M. is grateful to the Medical Research Council for a grant for scientific assistance.

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